Pedobiologia 33, 91–100 (1989)
VEB Gustav Fischer Verlag Jena

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Acceptability of pteridophyte litters to *Lumbricus terrestris* and *Oniscus asellus*, and implications for the nature of ancient soils

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With 3 figures

(Accepted: 88-10-19)

1. Introduction

Over recent years increasing attention has been devoted to feeding relationships between arthropods and pteridophytes, both in living, modern forms (eg. BALICK *et al.*, 1979; AUERBACH & HENDRIX, 1980; HENDRIX, 1980; HENDRIX & MARQUIS, 1983; OTTOSSON & ANDERSON, 1983 a, 1983 b) and in the fossil record (SCOTT & TAYLOR, 1983; TAYLOR & SCOTT, 1983). However, apart from GERSON's (1983) investigation into the breakdown of 26 pteridophyte species by a soil mite little published information is available on consumption of pteridophyte litter by terrestrial animal saprovores.

This paper presents a technique for measuring the consumption of pteridophyte litters by a common arthropod saprovore, the woodlouse *Oniscus asellus* L., and describes the acceptability to *Oniscus* of selected pteridophyte litters, in comparison with those of selected common tree species. An important aspect of the decay of soft plant materials in temperate woodlands is their burial and consumption by the earthworm *Lumbricus terrestris* L. This paper further describes the results of experiments to compare burial rates of pteridophyte and tree litters by *Lumbricus*.

Pteridophytes form a substantial minor component of modern terrestrial plant communities, and were a dominant component of certain ancient floras. The possible implications of the acceptability of pteridophyte litter for the nature of ancient soils will be discussed.

2. Materials and methods

2.1. *Oniscus* feeding trials

At appropriate times of year freshly fallen leaves of *Acer pseudoplatanus* L., *Alnus glutinosa* (L.) GAERTN., *Fraxinus excelsior* L. (known to be taken readily by animal saprovores), *Fagus sylvatica* L. and *Quercus petraea* (MATTUSCHKA) LIEBL. (rarely consumed when newly fallen) were collected on and around the University campus. Freshly senescent shoots of *Equisetum palustre* L. and *E. arvense* L. were also collected, and newly senescent fronds of *Athyrium filix-femina* (L.) ROTH, *Dryopteris dilatata* (HOFFM.) A. GRAY, *D. filix-mas* (L.) SCHOTT, *Osmunda regalis* L., *Phyllitis scolopendrium* (L.) NEWM., *Polypodium vulgare L.*, *Polystichum aculeatum* (L.) ROTH and *Pteridium aquilinum* (L.) KUHN. In all cases several plants at various sites were sampled, the material being rapidly air-dried at 20°C and stored at 20°C until required.

The relative acceptability of each litter type to *Oniscus* was assessed using animals collected from a mixed deciduous woodland and maintained on a diet of mixed deciduous tree litter in the laboratory at 20°C (mean fresh body mass (± SE) 78 ± 5 mg). Each choice chamber comprised a 12 cm square, 15 mm deep, wooden box with circular 21 mm diameter, 7 mm deep cells drilled in a 4 × 4 array in the floor. Each cell was lined

with a foil cup containing a disc of moist filter paper on which a piece of test material was placed. The chamber roof consisted of a layer of moist plastic foam held in place with a sheet of glass.

In each of 8 choice chambers weighed pieces of each of the 15 plant species (approximately 10 mg in mass) were placed in separate cells, the remaining cell being left empty. The positions of the fragments were varied systematically to eliminate bias due to location. Six *Oniscus* were introduced into each chamber, and allowed to feed for 6 d at 20°C. Filter papers and foam tops were remoistened daily. The fragments remaining were air dried at 20°C for 3 d and reweighed. In separate containers pieces of each type were kept on moist filter papers for 6 d and mass losses in the absence of woodlice measured (i.e. losses due to leaching, decay, and differences in moisture content a the start and end of the experiment), so that the amount of mass loss attributable to litter consumption by *Oniscus* could be calculated.

To assess the effects of decay on litter acceptability, pteridophyte fragments were weighed, then cultured in a saturated atmosphere on moist filter paper at 20°C for 22 d before being used as before. The *Oniscus* employed in this experiment weighed 76 ± 1 mg.

The acceptability of litter extracts was determined as follows: 9.5 mm diameter discs were cut from each of 8 air-dried, partly decayed leaves of *Acer pseudoplatanus*, and soaked in litter extracts or distilled water. Extracts were prepared by drying litter at 50°C overnight, cutting and grinding to pass a 2 mm mesh, extracting 1 g samples over 24 h with 10 ml aliquots of distilled water, and removing clear liquid with a fine pipette. Two discs from each of the 8 leaves were placed in 4 ml of extract or distilled water and left to dry at 20°C over 2 d. The discs were used in the same way as litter fragments in the previous experiments. The *Oniscus* in this experiment, weighing 93 ± 2 mg, were allowed to feed for 5 d.

The percentage mass losses recorded in tables 1–3 have been corrected for losses in controls without woodlice. Means for different species were compared using Student's t test after arcsin transformation.

2.2. *Lumbricus* feeding trials

Adult and large immature specimens of *Lumbricus* (fresh mass 4.6 ± 0.2 g) were collected by formalin expulsion from mixed deciduous woodland and kept for 3 d in soil to recover before use. Litter acceptability was assessed with a modified form of the technique described by SATCHELL & LOWE (1967). Pairs of earthworms were placed in plastic pots containing approximately 1.5 kg loam (soil surface area 150 cm^2) and left in the dark for one day to establish burrows. Four 1 cm square pieces of *Acer*, *Fagus* and *Fraxinus* leaves were soaked in distilled water and placed on the soil surface in each pot, together with 4 fragments from each of 5 pteridophytes, estimated by eye to be of similar size to the tree litter fragments. Two sets of trials (9 or 10 replicates per trial), with different pteridophyte species, were run simultaneously (see fig. 1 for species used in each set). In these, and subsequent, feeding trials with *Lumbricus* the post were kept in the dark at 10°C and numbers of fragments remaining unburied (i.e. not pulled down burrows so far as to be entirely below the general level of the soil surface) recorded at daily intervals.

To assess the effects of decomposition on acceptability, pieces of pteridophyte litter were incubated in a moist chamber at 20°C for 22 d prior to exposure to the earthworms. Finally, 1 cm squares of filter paper were soaked in litter extracts or distilled water (see *Oniscus* feeding trials) and used in place of litter fragments. Each square was labelled 4 times on each side with a pencilled identifying letter to ensure that ist could be recognised even when discoloured, damaged or partly buried. Burial of filter papers was rapid and this experiment was terminated after 5 d; trials with leaf pieces lasted 10 d. In all cases burial rates were compared between species using the χ^2 test or Fisher's Exact Probability Test.

3. Results

3.1. *Oniscus* feeding trials

Mass losses of control litter fragments in the first 2 experiments were relatively low, averaging only 7% after 6 d and 13% after 28 d. In the leaf extract experiment, percentage dry mass losses of ungrazed *Acer* discs over 5 d were significantly greater ($P < 0.01$) for those soaked in *Alnus* and *Fraxinus* extracts (21 and 22%) than for those soaked in extracts of other trees (6–8%), ferns (5–10%) or distilled water (3%). Those soaked in *Equisetum* extracts were intermediate at 14 and 15%. This suggests that some leaves yielded considerably greater amounts of extract, which were taken up by *Acer* discs and subsequently lost by leaching, than others.

In the trials with leaf litter fragments there was a large amount of variation between species in % dry weight loss attributable to *Oniscus* feeding (tables 1 and 2). In contrast, for *Acer* discs treated with litter extracts or distilled water (table 3) the variation between treatments was comparatively low (analysis of variance: $SS_{treatments} = 20\%\ SS_{total}$). In the latter experiment the overall variation

Table 1. Percentage dry mass losses, attributable to woodlouse feeding, of freshly remoistened leaf litter fragments exposed in separate cells within a common chamber to *Oniscus asellus* for 6 days, acceptability assessed as high (++), moderate (+) or low (–), and number of faecal pellets collected from each cell.

Plant species	Mass loss [%]	Acceptability	Pellets
Fraxinus excelsior	66 ± 11 a	++	24 ± 11 ab
Alnus glutinosa	55 ± 12 ab	++	28 ± 7 a
Athyrium filix-femina	47 ± 14 abc	++/+	29 ± 11 ab
Polypodium vulgare	35 ± 6 bc	+	23 ± 5 ab
Phyllitis scolopendrium	35 ± 14 abcd	+	21 ± 4 ab
Pteridium aquilinum	32 ± 11 bcd	+	22 ± 7 ab
Acer pseudoplatanus	28 ± 10 bcde	+	13 ± 4 ab
Osmunda regalis	25 ± 10 bcde	+	18 ± 2 ab
Equisetum arvense	21 ± 12 cdefg	+	14 ± 3 ab
Dryopteris dilatata	13 ± 4 cdef	+/–	18 ± 7 ab
Equisetum palustre	11 ± 7 def	+/–	13 ± 3 ab
Dryopteris filix-mas	8.8 ± 5.5 efg	+/–	18 ± 5 ab
Polystichum aculeatum	2.3 ± 1.4 gh	–	11 ± 4 bc
Quercus petraea	2.1 ± 0.9 gh	–	11 ± 3 b
Fagus sylvatica	1.5 ± 0.7 gh	–	15 ± 3 ab
Mean	26 ± 5		19 ± 2
Empty cell	–		17 ± 6 ab
Outside cells	–		19 ± 2 ac

Note: Tree species in bold type. Means ± S.E. Values sharing a common letter are not significantly different ($P > 0.05$). n = 8.

Table 2. Percentage dry mass losses, attributable to woodlouse feeding, of pteridophyte fragments cultured in a moist chamber, and freshly remoistened tree leaf litter fragments, exposed in separate cells within a common chamber to *Oniscus asellus* for 6 days, acceptability assessed as high (++), moderate (+) or low (–), and number of faecal pellets collected from each cell.

Plant species	Mass loss [%]	Acceptability	Pellets
Pteridium aquilinum	62 ± 10 a	++	27 ± 7 ab
Dryopteris dilatata	60 ± 9 a	++	26 ± 8 abc
Polypodium vulgare	54 ± 12 ab	++	34 ± 11 abd
Phyllitis scolopendrium	53 ± 8 abc	++	43 ± 10 a
Fraxinus excelsior	53 ± 10 abc	++	25 ± 7 ab
Alnus glutinosa	41 ± 9 abcd	++	11 ± 4 be
Athyrium filix-femina	34 ± 6 bc	++	30 ± 10 abe
Osmunda regalis	31 ± 9 cde	++	23 ± 6 abd
Equisetum arvense	16 ± 3 de	+	11 ± 4 be
Dryopteris filix-mas	12 ± 4 efg	+	18 ± 2 bf
Equisetum palustre	12 ± 4 ef	+	9.3 ± 2.8 cde
Acer pseudoplatanus	6.4 ± 1.1 fg	+	8.0 ± 1.6 ce
Polystichum aculeatum	4.0 ± 2.5 gh	+/–	15 ± 3 bef
Quercus petraea	1.0 ± 0.5 h	–	9.0 ± 2.4 cde
Fagus sylvatica	0.0 ± 0.0 i	–	10 ± 5 be
Mean	29 ± 6		20 ± 3
Empty cell	–		6.0 ± 3 e
Outside cells	–		20 ± 2 af

Note: Tree species in bold type. Means ± S.E. Values sharing a common letter are not significantly different ($P > 0.05$). n = 8.

between treatments was statistically significant ($P < 0.05$) although no 2 individual treatments differed significantly.

Leaves of *Alnus* and *Fraxinus* proved consistently highly acceptable, those of *Fagus* and *Quercus* unacceptable, with those of *Acer* intermediate (tables 1 and 2). However, *Alnus* extract came lowest in the order of consumption (table 3). Leaves of *Athyrium*, *Phyllitis*, *Polypodium* and *Pteridium* were readily consumed but those of *Polystichum* were rarely taken (tables 1 and 2). Moist chamber culture markedly increased overall acceptability (tables 1 and 2).

Table 3. Percentage dry mass losses, attributable to woodlouse feeding, of sycamore leaf discs soaked in distilled water (control) or leaf extracts and exposed in separate cells within a common chamber to *Oniscus asellus* for 5 days.

Plant species	Mass loss [%]
Dryopteris dilatata	27 ± 9
Fraxinus excelsior	26 ± 9
Athyrium filix-femina	26 ± 9
Pteridium aquilinum	24 ± 6
Acer pseudoplatanus	22 ± 9
Polystichum aculeatum	22 ± 8
Dryopteris filix-mas	21 ± 6
Quercus petraea	21 ± 8
Fagus sylvatica	21 ± 11
Equisetum arvense	18 ± 10
Osmunda regalis	18 ± 7
Polypodium vulgare	18 ± 9
Phyllitis scolopendrium	18 ± 2
Equisetum palustre	15 ± 7
Alnus glutinosa	11 ± 5
Control	17 ± 7
Mean	20 ± 1

Note: Tree species in bold type. No pairs of values are significantly different ($P > 0.05$). $n = 8$.

There was a high positive correlation between total numbers of faecal pellets deposited in each cell and % mass loss. Excluding empty cells, $r = 0.83$ for freshly remoistened fragments and 0.78 for moist chamber cultured fragments ($P < 0.001$). However, substantial numbers of pellets were deposited in empty cells (tables 1 and 2, 90% and 30% respectively of the mean number in cells containing litter).

3.2. *Lumbricus* feeding trials

Again, leaf fragments of *Fraxinus* proved very acceptable, with those of *Acer* moderately acceptable and *Fagus* fragments taken much less readily (figs. 1 and 2, table 4). In contrast, filter paper squares soaked in *Fraxinus* extract were least readily buried of the 3 tree species. Fragments of *Athyrium*, *Phyllitis*, and *D. dilatata* were rapidly buried (figs. 1 and 2, table 4) while those of *Polystichum* were rarely taken.

Moist chamber culture had a less marked effect than in the *Oniscus* feeding trials but *Osmunda* and *Pteridium* markedly increased in acceptability (figs. 1 and 2, table 4). Filter paper squares soaked in distilled water were slow to disappear (table 4, fig. 3). Extracts of *Phyllitis*, *Osmunda* and *E. palustre* considerably enhanced acceptability while *Polypodium* extract proved unacceptable (table 4, fig. 3).

4. Discussion

Burial rates of leaf fragments and filter papers provided a convenient day-to-day measure of acceptability to *Lumbricus*. However, although numbers of *Oniscus* faecal pellets were strongly positively correlated with litter consumption over the duration of the feeding trials, pellet counts did

Table 4. Acceptability to *Lumbricus terrestris* of freshly remoistened leaf litter fragments, leaf litter fragments cultured under moist conditions, and filter paper squares soaked in leaf extracts, assessed as high (++), moderate (+) or low (−).

Series	Freshly remoistened litter Spp.		Accepta-bility	Moist-cultured litter Spp.		Accepta-bility	Filter paper fragments Spp.		Accepta-bility
A	*Phyllitis scolopendrium*	a	++	*Phyllitis scolopendrium*	a	++	*Phyllitis scolopendrium*	a	++
	Dryopteris dilatata	ab	++	*Dryopteris dilatata*	ab	++	*Osmunda regalis*	a	++
	Equisetum palustre	bc	++	*Osmunda regalis*	bcd	++	*Equisetum palustre*	b	++/+
	Fraxinus excelsior	c	++	***Fraxinus excelsior***	c	++	*Pteridium aquilinum*	bc	++/+
	Acer pseudoplatanus	d	+	*Pteridium aquilinum*	d	++/+	***Acer pseudoplatanus***	cd	+
	Osmunda regalis	de	+/−	*Equisetum palustre*	e	++/+	*Dryopteris dilatata*	cd	+
	Pteridium aquilinum	de	+/−	***Acer pseudoplatanus***	e	+	Control (dist. water)	de	−
	Fagus sylvatica	e	−	***Fagus sylvatica***	f	−	***Fagus sylvatica***	d	−
							Fraxinus excelsior	e	−
B	*Athyrium filix-femina*	a	++	*Athyrium filix-femina*	a	++	***Acer pseudoplatanus***	ab	+
	Equisetum arvense	b	++	***Fraxinus excelsior***	b	++	*Dryopteris filix-mas*	ac	+
	Fraxinus excelsior	b	++	*Dryopteris filix-mas*	bc	++/+	*Equisetum arvense*	cd	+
	Dryopteris filix-mas	c	+	*Polypodium vulgare*	c	++/+	***Fagus sylvatica***	e	+/−
	Acer pseudoplatanus	c	+	*Equisetum arvense*	c	++/+	*Polystichum aculeatum*	de	+/−
	Polypodium vulgare	c	+	***Acer pseudoplatanus***	c	++/+	***Fraxinus excelsior***	ef	+/−
	Fagus sylvatica	d	−	***Fagus sylvatica***	d	−	*Athyrium filix-femina*	f	−
	Polystichum aculeatum	d	−	*Polystichum aculeatum*	d	−	Control (dist. water)	f	−
							Polypodium vulgare	f	−

Note: Tree species in bold type. For species sharing a common letter the proportions of fragments buried are not significantly different ($P > 0.05$). $n = 9$ for moist-cultured litter series B, 10 for rest.

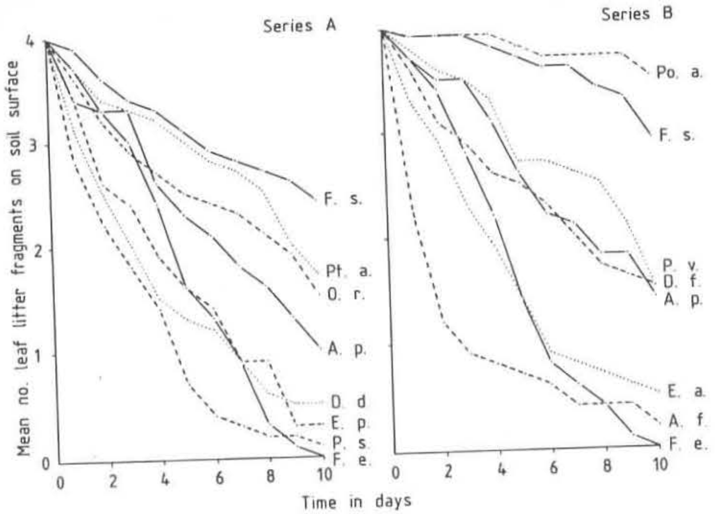

Fig. 1. Burial of freshly remoistened leaf litter fragments by *Lumbricus terrestris* (A.f.) *Athyrium filix-femina*, (A.p.) *Acer pseudoplatanus*, (D.d.) *Dryopteris dilatata*, (D.f.) *Dryopteris filix-mas*, (E.a.) *Equisetum arvense*, (E.p.) *E. palustre*, (F.e.) *Fraxinus excelsior*, (F.s.) *Fagus sylvatica*, (O.r.) *Osmunda regalis*, (P.s.) *Phyllitis scolopendrium*, (P.v.) *Polypodium vulgare*, (Po.a.) *Polystichum aculeatum*, (Pt.a.) *Pteridium aquilinum*. n=10.

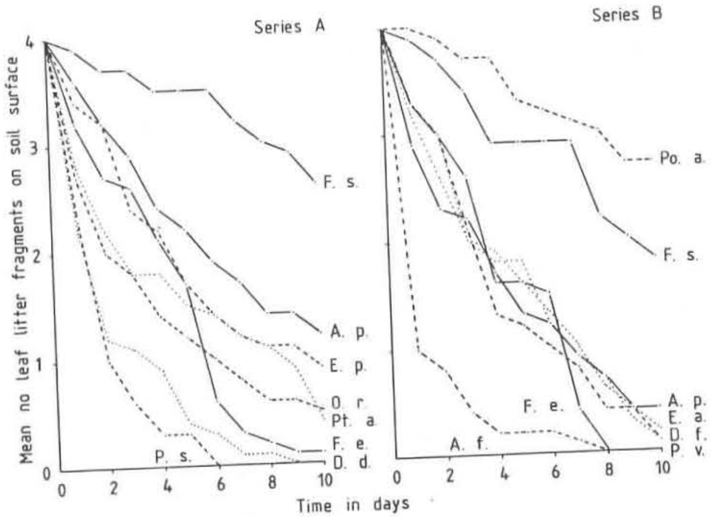

Fig. 2. Burial by *Lumbricus terrestris* of pteridophyte fragments cultured in a moist chamber and freshly remoistened tree leaf litter fragments. Abbreviations as fig. 1. Series A n=10, Series B n=9.

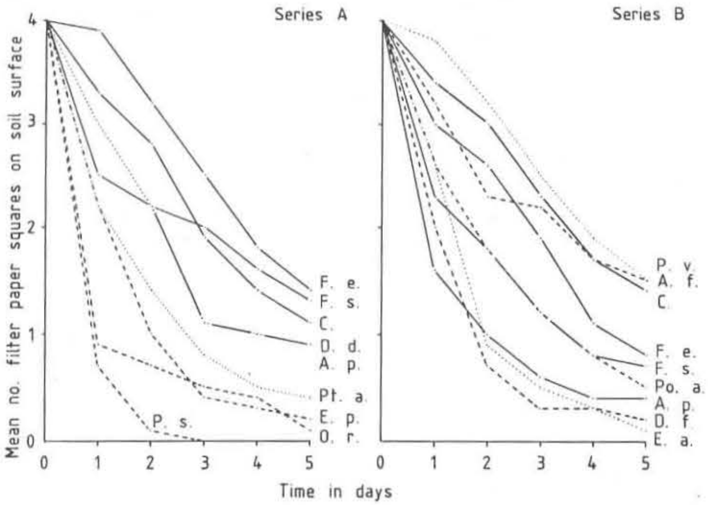

Fig. 3. Burial by *Lumbricus terrestris* of filter paper squares soaked in distilled water (control, C.) or leaf extracts. Abbreviations as fig. 1. n=10.

not give a reliable estimate of day-to-day consumption of leaf material under the conditions of these experiments. Litter mass losses provided a useful measure of relative consumption of each litter type by the woodlice. Removal of faecal pellets for daily counting prevented the possibility of coprophagy. However, since isopod pellets are consumed usually after a period of decay (HASSALL & RUSHTON, 1985) it seems unlikely that feeding behaviour was significantly affected over the short duration of these experiments.

Relative acceptabilities of tree litters determined in this study are similar to those reported elsewhere (eg. SATCHELL & LOWE, 1967; EDWARDS, 1974). The attractiveness of different test materials will depend in part on their physical properties. The soft laminae of fern pinnae and tree leaves were consumed before the veins. The delicate fronds of *Athyrium* were readily buried and consumed while the hard, prickly pinnae of *Polystichum* were generally unacceptable (tables 1, 2 and 4, figs. 1 and 2), although *Polystichum* extracts were moderately acceptable (tables 3 and 4, fig. 3). *Phyllitis* was readily taken (tables 1, 2 and 4, figs. 1 and 2) despite its thick, fleshy leaves; filter papers containing *Phyllitis* extract were rapidly buried by *Lumbricus* (table 4, fig. 3). Similarly, the rigid nature of sections of *Equisetum* stem did not prevent *Lumbricus* from readily pulling them down into its burrows (table 4, figs. 1 and 2).

Filter papers soaked in distilled water were slow to disappear compared with those containing pteridophyte extracts (table 4, fig. 3), suggesting that water soluble substances in pteridophyte litter generally have a positive influence on acceptability. SATCHELL & LOWE (1967) reached a similar conclusion regarding tree litters. Possible distasteful substances include defensive compunds against herbivores, a wide range of which has been recorded for ferns (COOPER-DRIVER, 1985). OTTOSSON & ANDERSON (1983a, 1983b) recorded a decline in concentration of defensive compounds with increasing age of fern fronds. GERSON (1983) found that feeding by a soil mite on, initially green, pteridophytes intensified when they became brown, and the acceptability of decaying leaves to earthworms, isopods and other macroarthropods has been shown to be greater than that of fresher ones (SATCHELL & LOWE, 1967; EDWARDS, 1974; HASSALL & RUSHTON, 1982). SATCHELL & LOWE (1967) related increased acceptability of tree leaves on weathering to reduced tannin concentrations, suggesting that the reduction might be largely due to microbial activity. The acceptability of dead leaves to *Lumbricus* is enhanced by the development of microbial populations (WRIGHT, 1972; COOKE & LUXTON, 1980; COOKE, 1983). In the current investigation dense fungal

mycelium was observed on the surface of litter in moist chamber culture, most prolific on *Equisetum*, and substantial on *Pteridium*.

Contemporary macrodecomposers of temperate regions, including isopods, diplopods and earthworms, are most abundant and diverse in moist (but not waterlogged), base-rich soils, playing a major part in the rapid decay, and incorporation into the mineral layers, of dead plant remains, and consequent development of mull soils. Formation of similar soils could presumably have occurred before the evolution of higher vascular plants in areas of base-rich parent materials and moderate to high precipitation providing that macrodecomposers were present and the plant litter was acceptable to them. Diplopod-like arthropods have a long fossil history, extending back to the Silurian (ALMOND, 1985) and, as trace fossils, possibly to the Late Ordovician (RETALLACK & FEAKES, 1987). Terrestrial isopods have a short fossil record, postdating the appearance of angiosperms (LITTLE, 1983), however it seems probable that they were much earlier colonisers of the land; terrestrial Oniscoidea may have appeared in the Carboniferous (VANDEL, 1965, 1972). Earthworms have a very fragmentary and inconclusive fossil record (CONWAY MORRIS *et al.*, 1982; LITTLE, 1983), but evidence suggests that terrestrial oligochaetes, ancestral Lumbricina, were probably present in the Palaeozoic, the various families having differentiated since the start of the Cretaceous (SIMS, 1980; TIMM, 1981; BOUCHÉ, 1983).

WILCKE (1955) related the appearance of fossil mull soils to the development of angiosperms. It is true that earthworms and other large saprovores are scarce in eg. coniferous woodlands, where mor soils are typical, compared with broadleaved woodlands, where mull soils frequently develop. However, it is by no means certain that more primitive plant communities could not have supported substantial macrodecomposer populations, including isopods and earthworms. RETALLACK (1985) and RETALLACK & FEAKES (1987) have recorded burrows, presumed to have been formed by soil-dwelling arthropods, in Late Ordovician palaeosols. The Carboniferous *Arthropleona,* resembling a giant polydesmid millipede, apparently fed on lycopod tissue (ROLFE, 1980), and fern spores and sporangia have been recorded in Carboniferous arthropod faeces (SCOTT & TAYLOR, 1983; TAYLOR & SCOTT, 1983).

The horsetails, and most ferns, tested in the present study were at least moderately acceptable to *Oniscus* and *Lumbricus*. This is consistent with the generally rapid rate of disappearance of horsetail and fern litters on mull soils in the field (personal observation). On the assumption that similar levels of acceptability prevailed prior to the evolution of angiosperms it seems plausible to suggest that mull-type soils may well have developed over base-rich rocks in moist regions prior to the appearance of flowering plants. The apparent absence of fossil evidence of this could be due to the fragmentary nature of the fossil record, which can give a misleading picture of the composition of ancient terrestrial communities (SCOTT, 1980; ROLFE, 1985) and may underrepresent the frequency of mull soils, which, by their very nature, are less likely to be detected in fossil form than soils rich in recognisable organic remains. It has been suggested (THOMAS, 1985) that one reason for the scarcity of fossil polypodiaceous ferns in the Tertiary may have been their occurrence in areas where the chances of fossilisation were negligible, the kinds of areas which many inhabit today. Clearly, further light could be thrown on the evolutionary origin of mull soils by additional investigations into the acceptability of pteridophytes to animal saprovores and the nature of soils under modern pteridophyte-dominated plant communities.

5. Acknowlegements

It is a pleasure to thank Mr. S. N. QUAYLE for practical assistance with the feeding trials, Professor J. B. WHITTAKER for commenting on the manuscript, and Mr. P. W. H. FLINT for drawing figs. 1–3.

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Synopsis: *Original scientific paper*

Piearce, T. G., 1989. Acceptability of pteridophyte litters to *Lumbricus terrestris* and *Oniscus asellus*, and implications for the nature of ancient soils. Pedobiologie **33**, 91–100.

Acceptability to the woodlouse *Oniscus asellus* L. and earthworm *Lumbricus terrestris* L. of litters of a fern and 2 horsetail species was assessed, in comparison with that of selected tree litters. Burial rates provided a convenient measure of acceptability to *Lumbricus*, weight losses of acceptability to *Oniscus*. Faecal pellet production by *Oniscus*, though positively correlated with litter consumption, did not give a reliable estimate of day-to-day litter removal. There was considerable interspecific variation in pteridophyte acceptability, but most litters proved at least moderately acceptable. *Phyllitis scolopendrium* (L.) Newm. leaf fragments were particularly readily consumed and buried while *Polystichum aculeatum* (L.) Roth fragments were taken least often. Litter acceptability increased after moist chamber culture. Possible implications for the nature of ancient soils are considered; it is suggested that mull soils may have developed, at least on a local scale, in ancient pteridophyte communities given suitable climatic conditions and parent materials.
Key words: Acceptability assays, Filicales, Equisetales, *Lumbricus terrestris*, *Oniscus asellus*, Palaeosols

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